DRAFT

Trophic interactions between *Cladophora glomerata*, associated epiphytes, and *Gammarus lacustris* in the Colorado River, Arizona, U.S.A.

DRAFT

PRELIMINARY SUBJECT TO REVIEW & CHANGE

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Running Head: Trophic interactions between *Cladophora* and *Gammarus*.

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SUMMARY

1. *Cladophora glomerata* is the dominant filamentous green alga in the tailwaters of the Colorado River, USA, below Glen Canyon Dam, but is replaced by filamentous cyanobacteria, *Oscillatoria* spp., below the confluence of the Paria River (26 km below the dam) where suspended sediments are elevated.

2. Benthic algal assemblages played an important role in the distribution of the amphipod, *Gammarus lacustris*, in the dam-controlled Colorado River through Grand Canyon National Park, Arizona. *Cladophora* and *G. lacustris* showed a weak positive relationship at 10 cobble-riffle habitats from Lees Ferry (0.0 km) to Diamond Creek (362 km), while no relationship was found between *Oscillatoria* spp. and *G. lacustris*.

3. The relationship between algal substrata and *G. lacustris* was tested by a series of *in situ* habitat choice experiments. *G. lacustris* showed a significant preference for *Cladophora* (with epiphytes) over *Oscillatoria* spp., detritus, and gravel in treatment pans at Lees Ferry.

4. Epiphytic diatoms (i.e., food) were the overriding determinant of subtratum choice by *G. lacustris* in laboratory experiments. *Gammarus* chose the *Cladophora*/epiphytic diatom community over sonicated *Cladophora* with reduced diatoms. The amphipods also chose string soaked in diatom extract over string without diatom extract.

5. Possible mutualistic interactions of this algal/herbivore relationship are discussed.

Introduction

Factors that influence habitat selection of amphipods in marine and freshwater ecosystems are diverse but commonly relate to food and shelter. Adequate refugia are critical for these highly abundant, relatively large and slow moving herbivores (Duffy, 1990). Host-plant specialization by amphipods based on secondary plant metabolites that defend animals from fish predation is well documented in marine ecosystems (Duffy & Hay, 1991; Hay, Duffy & Fenical, 1987, 1990; Hay et al., 1988; Paul & Van Alstyne, 1988), and to some extent in freshwater ecosystems (Newman et al., 1990). Both spatial and structural components of plant architecture influence habitat selection by marine amphipods (Teker, 1985; Hacker & Steneck, 1990). Host-plant architecture, also influences distribution of the marine amphipod, Gammarellus anglous (Hacker & Steneck, 1990). Several investigators (Strong, Lawton & Southwood, 1984; Price, et al., 1980) report similarities between terrestrial plant-herbivore interactions and marine amphipod herbivores.

Amphipods play a significant role in nutrient cycling and energy flow in streams, from leaf pack decomposition through consumption of associated fungi and bacteria (Barlocher & Kendrick, 1973; Marchant & Hynes, 1981). Diet and feeding strategies vary widely among amphipods. Diet includes fungi (Willoughby & Sutcliffe, 1976; Willoughby & Earnshaw, 1982; Barlocher & Kendrick, 1973), bacteria (Grimm & Fisher, 1989), detritus (Nilsson 1974), nannoplankton (Blinn & Johnson, 1982); invertebrates (Moore, 1977), macrophytic algae (Deksbakh & Sokolova, 1965; Hudon, 1983), and epiphytic diatoms (Moore 1975; 1977; Blinn et al., 1992; Pinney, 1992). Diet selection is typically considered a function of body size and taxon specific feeding mechanisms (Hudon, 1983).

Macroalgae provide herbivores with food, either directly or indirectly (Gregory, 1983), and provide a high surface area for attachment of filter feeders, predators, and grazers (Minshall, 1984). Filamentous algae alter microhabitat conditions by modifying current, blocking light, altering dissolved oxygen, and collecting detritus (Dodds, 1991a): changes which influence macroinvertebrates on a taxon specific basis (Towns, 1981). Mutualisms between aquatic herbivores and macroalgae may exist (Dodds, 1991b), with herbivores removing sediments and light-limiting epiphytes and providing soluble nutrients to filamentous algae like *Cladophora glomerata*.

This investigation describes the importance of *C. glomerata* and associated epiphytic diatoms to the distribution of *Gammarus lacustris* in the dam-controlled Colorado River through Grand Canyon, USA. *Gammarus lacustris* biomass is positively correlated with biomass of *C. glomerata*. *Oscillatoria* spp. and detritus are also common substrata in this large river, however there was no correlation between biomass of *G. lacustris* and biomass of these substrata. Field and laboratory experiments were conducted to test the relationship between *G. lacustris* and various substrata in the Colorado River.

Materials and Methods

The distribution of *Cladophora glomerata*, *Oscillatoria* spp., detritus, and *Gammarus lacustris* biomass were determined bimonthly during 1991 at 10 cobble-riffle sites in the dam-controlled Colorado River from Lees Ferry (River Kilometer = (RK) 0.0) to Diamond Creek (RK 362; Stevens, 1983; Blinn *et al*., 1992). Three replicated samples were taken with a Hess sampler, sorted live within 24 hrs of collection and oven-dried at 60°C to a constant mass. An ash-free dry weight (AFDW) conversion was determined for *Cladophora* by ashing 60 samples for one hr at 500°C and re-weighing:

$$AFDW = 0.34825\ (\text{dry wt.}) + 0.04912$$

$$(R^2 = 0.923;\ F_{1,58} = 707.79,\ p < 0.001).$$

All *Oscillatoria* spp. samples were ashed and are reported as AFDW.

The abundance of *G. lacustris* within tufts of *C. glomerata* with and without the associated diatom community was investigated at Lees Ferry, Arizona. Ten 150 g tufts of *C. glomerata* with diatoms, and ten 150 g tufts of *C. glomerata* without diatoms were randomly collected and examined for *G. lacustris*. Diatom composition and density were determined with a Sedgwick-Rafter chamber.

Field experiments

Field experiments were conducted at Lees Ferry, Arizona to test the choice by *G. lacustris* for four common substrata in the Colorado River ecosystem. These substrata included: *C. glomerata*, *Oscillatoria* spp., detritus, and gravel as a control. Round galvanized pans (100 cm^2 and 16 cm deep) were divided into four equal sections with 3 cm PCV secured with sheet metal screws and sealed with silicone caulk. A saw kerf was cut into each section and a 1 cm screen mesh 10 cm high was placed between sections to reduce lateral movement. These mesh "fences" were five cm below the rim of the pan so amphipods could choose freely between substrata. Water flow through the pan was enhanced with three holes (2 cm diameter) drilled into each section. The entire pan was covered with one mm nylon mesh secured with large rubber bands. A random block design was used for the arrangement of substrata in each pan. Three blocks of eight pans (n = 24) were placed in shallow (<60 cm) water at Lees Ferry (<0.2 m/sec). Each block was 2 m apart and every pan was 1 m apart on center.

Cladophora glomerata and Oscillatoria spp. substrata were collected from a cobble bar at Lees Ferry and detritus was gathered from the Paria River, 1.2 km below Lees Ferry. Gravel (0.5 to 1.5 cm in diameter) was collected at Lees Ferry and sterilized. Macroinvertebrates were removed from algal and detrital substrata and an estimated uniform volume of each substratum (90 cm^3) was used for each category.

Sterilized gravel (0.5 cm deep) was distributed across the bottom of each section. Twenty-four amphipods (15-20 mm) were placed into each experimental pan. This number of amphipods was derived from one standard deviation of the annual mean density of G. lacustris in C. glomerata at Lees Ferry, AZ (n = 6, df = 18) (Blinn et al., 1992). Experiments were conducted for one hr at

1200, 1500, and 1900 hrs in situ at Lees Ferry to compare light and dark treatments. Amphipods were released in the center of treatment pans for 1200 and 1900 hr experiments, while animals were released in randomly chosen habitats in the 1900 hr experiment.

Laboratory experiments

A series of laboratory substratum choice experiments were conducted in plastic containers (30 x 12 x 12 cm) with 1.5 L of filtered river water. Each container was divided into three sections with 1 cm mesh screen caulked into place. Substratum types were placed at each end of the containers. The chambers were incubated at 50 μEin m^{-2} sec^{-1} for four and eight hrs at 10°C, the mean annual temperature of the Colorado River (Blinn et al., 1992). Cladophora glomerata with diatoms, Cladophora with reduced diatoms, and amphipods were collected at the Lees Ferry cobble bar (0.8 km). All macroinvertebrates were removed from C. glomerata (150 gms wet wt.) before placing into chambers. Each experiment was scored as C. glomerata, string, and center (no preference).

Three habitat choice experiments were conducted in the laboratory with G. lacustris. In the first experiment, G. lacustris was given a choice of C. glomerata with associated diatoms and sonicated C. glomerata with reduced diatoms. Cladophora glomerata were sonicated (Bransonic 35) in river water for five min to remove epiphytic diatoms. Microscopic observations determined this procedure removed at least 80% of the epiphytic diatoms. Two trials were run with six containers and 15 amphipods and another two trials were run with five containers. Both sets of trials were examined at four and eight hours under light and dark conditions.

In a second laboratory experiment, G. lacustris were given a choice of string soaked for 24 hr in epiphytic diatom extract and string soaked in filtered river water. Cotton string (15 gm dry wt), 1 mm in diameter, was used to simulate the plant structure of C. glomerata. Two trials with each string treatment were run with five containers and 15 amphipods and two trials were run with eight containers and 25 amphipods. Both sets of trials were scored at four and eight hr under light and dark conditions.

In the third experiment, G. lacustris was offered the choice of C. glomerata with diatoms and string soaked in filtered river water. This trial tested for the effect of string. Sets of 25 amphipods were placed into eight containers for two trials and scored at four and eight hours under light and dark conditions.

Statistical analyses

Multiple regression analyses were used to analyze field collection data to determine the relationship between C. glomerata, Oscillatoria spp., detritus, and G. lacustris biomass. The Friedman random block design test was used to analyze field habitat selection experiments with predictor variables of C. glomerata, Oscillatoria, detritus, and gravel. Gammarus lacustris density was the response variable. These data were also analyzed by ANCOVA with depth and current velocity as covariates. A post hoc HSD Tukey test was used to determine differences between treatments. Laboratory substratum selection experiments were analyzed using the Kruskal-Wallace non-parametric test, with substratum type the predictor variables and Gammarus density the response variable. MANOVA was used to determine the effect of light and duration of experimental runs on Gammarus substratum preference. All calculations were performed with SYSTAT computer software (Version 5.1, Wilkinson, 1989).

Results

Although highly variable, biomass of Gammarus lacustris was significantly ($F_{3,397} = 103.5$, $p < 0.001$) correlated with biomass of Cladophora glomerata in the Colorado River between Lees Ferry and Diamond Creek (Fig. 1). In contrast, G. lacustris biomass showed no correlation with Oscillatoria biomass ($F_{3,397} = 0.19$, $p = 0.38$; or detritus ($F_{3,397} = 0.76$, $p = 0.65$), both common substrata below the confluence of the Paria River.

Field observations at Lees Ferry indicated significantly higher numbers of G. lacustris in tufts of C. glomerata with epiphytic diatoms (brown in color) than in C. glomerata with reduced densities (bright green in color) of epiphytic diatoms ($F_{1,19} = 11.361$, $p = 0.003$). Cladophora with epiphytes had 3-fold more amphipods than C. glomerata with reduced epiphytic diatoms. Average cell density of epiphytic diatoms for the C. glomerata/epiphyte association was 14,400 cells/150 g Cladophora (wet wt), while average epiphyte density on Cladophora with reduced epiphytes was <2,500 cells/150 g Cladophora. The composition of the epiphytic diatom community on C. glomerata was dominated by Diatoma vulgare, D. tenue, and Fragilaria spp.

Habitat choice experiments conducted at Lees Ferry concurred with the positive relationship between G. lacustris and C. glomerata. Cladophora glomerata was selected by G. lacustris over Oscillatoria spp., detritus, and gravel (Fig. 2). Application of the Friedman non-parametric test (145.7, $p < 0.0001$) resulted in the following rank sums: C. glomerata = 283, Oscillatoria spp. = 193, detritus = 137.5, and sterile gravel (control) = 110. Pairwise comparisons of each habitat showed a significant difference in G. lacustris abundance (Tukey HSD $p < 0.0001$) except for detritus and gravel. There was no significant difference between experiments ($F_{2,285} = 1.08$, $p = 0.33$), therefore all in situ experiments were pooled. Also, depth and current velocity did not alter habitat choice by G. lacustris over a range in depth of 10-37 cm and current velocities of 0-0.18 (Table 1).

Laboratory choice experiments provided evidence that epiphytic diatoms play an important role in the positive relationship between G. lacustris and C. glomerata in the Colorado River (Table 2). G. lacustris preferred C. glomerata with epiphytic diatoms over sonicated C. glomerata, with reduced epiphytic diatoms ($F_{2,39} = 218.16$ $p < 0.0001$). G. lacustris also selected string soaked in diatom extract over plain string ($F_{3,16} = 25.7$, $p < 0.001$), suggesting that epiphytic diatoms provide a strong attraction for G. lacustris. Finally G. lacustris preferred C. glomerata with diatoms over extract-free string ($F_{2,60} = 39.4$, $p < 0.0001$).

Discussion

Although variable, the distribution of Gammarus lacustris is positively correlated with the distribution of the green filamentous alga, Cladophora glomerata, and its epiphytic diatom assemblage in the Colorado River through Grand Canyon. In situ habitat choice experiments support these findings: G. lacustris chooses C. glomerata over Oscillatoria, detritus or gravel in a 3:1:1:1 ratio, respectively.

The overriding importance of epiphytic diatoms on C. glomerata (as food) was demonstrated in both field observations and laboratory choice experiments. There was a significant preference by G. lacustris for tufts of C. glomerata with epiphytic diatoms over C. glomerata tufts of similar size with reduced epiphytic diatoms. Also, G. lacustris preferred string soaked in diatom extract over string soaked in Colorado River water. Over 95% of the diet of G. lacustris at Lees Ferry are epiphytic diatoms associated with C. glomerata; <1% of the diet is composed of C. glomerata (Pinney, 1991). Patrick and co-workers (1983) suggested that Cladophora may not be readily consumed by macroinvertebrates because it is a relatively poor food source, however Dodds and Gudder (1992) report that several freshwater invertebrates consume Cladophora.

Therefore, our data suggest that epiphytic diatoms may provide chemical cues for G. lacustris. The epiphytic diatom assemblage chemically attracts the herbivore (G. lacustris) into the C. glomerata assemblage. Other interactions between Cladophora and epiphytes have been reviewed by Dodds and Gudder (1992).

The highly variable and somewhat weak relationship between G. lacustris and C. glomerata results from complex interactions between substratum (Cladophora), food (epiphytic diatoms), and G. lacustris throughout the Colorado River. These interactions confuse the association between C. glomerata and G. lacustris. Cladophora glomerata tufts with high densities of epiphytic diatoms are likely to show strong positive associations with G. lacustris, while tufts with low epiphytic densities may have reduced numbers of amphipods.

The high standing crop of C. glomerata in the tailwater reach is due, in part, to abundant armoured substrata and the hypolimnetic release of constantly cold, clear water from Glen Canyon Dam (Stanford & Ward, 1991). The decrease in standing stock of G. lacustris with distance from Glen Canyon Dam (Blinn & Cole 1991; Blinn et al., 1992) corresponds with a decrease in C. glomerata biomass and associated epiphytic diatoms down river (Hardwick et al., 1992). The decrease and variable distribution of both C. glomerata and associated epiphytic diatoms is attributed to an increase in suspended sediment load below two major tributaries in the Grand Canyon, i.e., Paria River (26 km below the dam) and the Little Colorado River (123 km below the dam) (Andrews, 1991), and river regulation (Usher & Blinn, 1990; Blinn et al., 1992; Hardwick et al., 1992).

While some marine amphipods select algal substrata for protection from predators (Duffy & Hay, 1991), G. lacustris may expose themselves to greater predation in the Colorado River by selecting Cladophora as a substratum. Rainbow trout (Leibfried, 1988) and waterfowl ( ) readily consume C. glomerata and associated amphipods in the Colorado River.

In contrast to some of the marine associations (Hay et al., 1987), the Gammarus/Cladophora association in the Colorado River is driven primarily by food. As noted by Bell (1991), there are also important amphipod/epiphyte linkages in marine ecosystems. In the Colorado River we consider C. glomerata to be the architectural host plant that provides a substratum for colonization by epiphytic diatoms, the food source

Although this system is complicated by possible mutualistic interactions, it generally conforms to Kogan's (1977) fifth model of chemical influences on plant/herbivore interactions in which host plant chemical cues are used by the herbivore as stimulants for host location and subsequent feeding or oviposition. For example, Cruciferae-feeding terrestrial Lepidoptera, Coleoptera and Diptera use mustard oils as cues to locate their host plants (Kogan, 1977).

Examination of interactions between C. glomerata, associated diatom epiphytes, and herbivores may reveal a mutualistic community. Epiphytes, growing on _C. glomerata_ attract herbivores. These herbivores, in turn consume epiphytes and detritus trapped by epiphytic diatoms, alter the light climate, and release mineralized nutrients which may be assimilated by the host plant (Dudley, 1986; Dodds, 1991b; Dodds & Gudder, 1992). Positive mutualistic interactions between marine macroalgae and amphipods have been documented by Brawley & Adey (1981) and Duffy (1990), however the potential mutualistic interaction between _C. glomerata_, epiphytes, and _G. lacustris_ in freshwater ecosystems requires further research (Dodds & Gudder, 1992). This form of mutualism is based on nutrient or food supply, and may be an important factor influencing aquatic benthic community structure.

Acknowledgements

Funds for this project were provided by the Bureau of Reclamation, Glen Canyon Environmental Studies (BOR) and the Cooperative Park Studies Unit of the National Park Service at Northern Arizona University, Flagstaff, Az (Contract # CA 8024-8-0002). Justin Carder, Gaye Oberlin, Jeanette Macauley, and Mike Shaver assisted in field data collections and choice experiments. We also thank Peter Price and Perry Thomas for helpful comments on earlier drafts of this manuscript.

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Table 1. ANCOVA analysis for the *in situ Gammarus lacustris* habitat selection experiment. Depth and current did not significantly affect the selection process. Habitat selection was highly significant, with *Cladophora glomerata* the preferred substratum.

SOURCE	SS	DF	MS	F	P
HABITAT	2228.3	3	742.7	139.6	<0.00001
DEPTH	0.1	1	0.1	0.02	0.887
CURRENT	515.8	1	1.68	0.31	0.575

Table 2. Results of Kruskal-Wallis one-way analysis of variance for laboratory selection experiments. The null hypothesis was rejected for each experiment and revealed the following: Experiment 1 showed that *Gammarus lacustris* selected *Cladophora glomerata* with associated epiphytic diatoms over sonicated *C. glomerata* with reduced epiphytes, Experiment 2 showed that *G. lacustris* preferred string soaked in epiphytic extract over string soaked in river water, and Experiment 3 showed that *G. lacustris* preferred *C. glomerata* over plain string, indicating that string (architecture) is not an attractant.

EXPERIMENT	H	PROBABILITY		
1	88.03	<0.0001	n = 127	df = 3
2	84.25	<0.0001	n = 105	df = 3
3	44.01	<0.0001	n = 64	df = 3

FIGURE LEGENDS

Figure 1. Regression analysis of Gammarus lacustris and Cladophora glomerata in the Colorado River through Grand Canyon. C. glomerata has a positive correlation for G. lacustris distribution on cobble/riffle habitats. Low regression value can be explained by the patchy distribution of C. glomerata with and without epiphytic diatoms.

Figure 2. Results of in situ habitat selection experiment with Gammarus lacustris at Lees Ferry, Arizona. The abscissa represents number of amphipods that selected various substrata. Cladophora glomerata was the preferred habitat over Oscillatoria spp. and detritus; ANOVA analysis ($F = 276.47$; $p < 0.0001$; $n = 72$; $\pm$ SD).

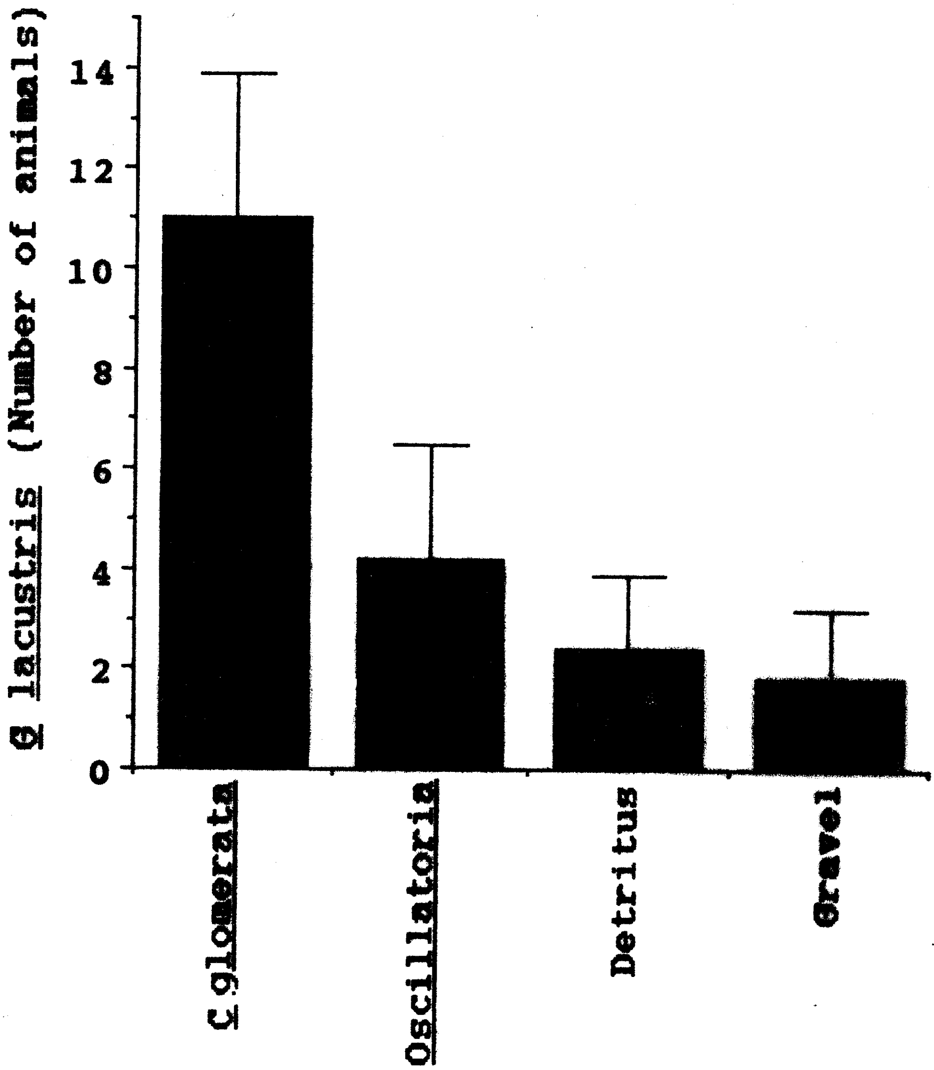
G lacustris (Number of animals)
0
2
4
6
8
10
12
14
C glomerata
Oscillatoria
Detritus
Gravel

Fig. 2.

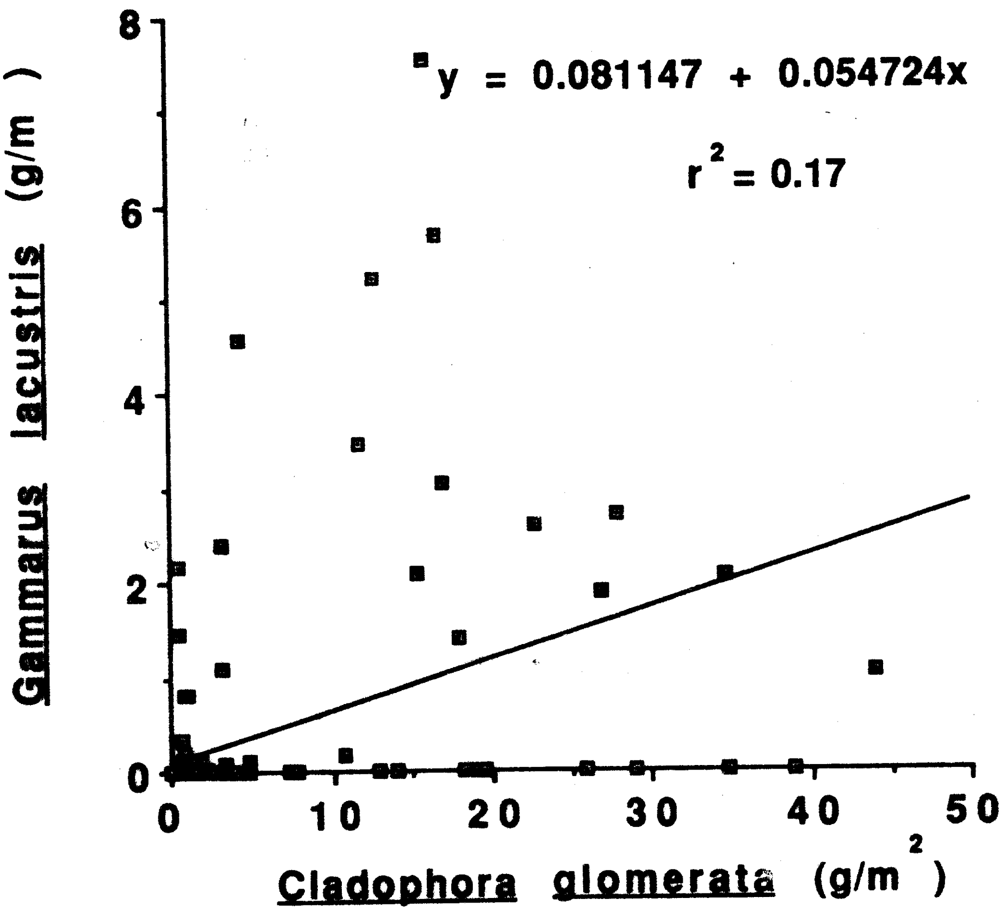
y = 0.081147 + 0.054724x
r² = 0.17
Gammarus lacustris (g/m²)
Cladophora glomerata (g/m²)
0
2
4
6
8
0
10
20
30
40
50

Fig 1